

INTERGRADATION OF HABITATS OF NON-VOLANT SMALL MAMMALS IN THE PATCHY CERRADO LANDSCAPE ¹

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ABSTRACT: The relevant literature on the community composition, population densities, habitat preference, and interspecific relations of small mammals in the Cerrado biome of central Brazil is surveyed, and their community structure in different habitats of the open savanna as well as in forested habitats, especially gallery forests, is analyzed. Small mammal communities differ along a gradient of natural habitats in the Cerrado landscape. There are habitat generalists occurring in more than three types of habitat (pan-habitat species) and habitat specialists, showing a high degree of fidelity to habitat. Most species are of the latter kind, displaying high habitat specificity. Habitat structure is the major factor determining small mammal communities within the Cerrado landscape. Community differences appear to be a function of local mosaic factors as well as differences among river basins, between high plateau forested habitats and lowland valley forests, or between moister open areas with soft soil and abundant grass versus very dry and rocky microhabitats.

Key words: Cerrado, conservation, habitats, marsupials, rodents, small mammals.

RESUMO: Intergradação de hábitats de pequenos mamíferos não-voadores na paisagem retalhada do bioma Cerrado.

Contribuições consistentes para o conhecimento dos pequenos mamíferos do bioma Cerrado do Brasil central são examinadas, especificamente sobre composição de comunidades, densidade de populações e preferência de hábitat. A estrutura de comunidade de pequenos mamíferos é analisada em hábitats diferentes do Cerrado aberto bem como em hábitats florestados das matas de galeria. As comunidades de pequenos mamíferos diferem num gradiente de hábitats da paisagem do Cerrado. Há espécies hábitat-generalistas que ocorrem em mais de três tipos de hábitats (espécies pan-habitativas) e espécies hábitat-especialistas, restritas a um tipo de hábitat, que compreendem a maioria das formas, indicando alta especificidade. Estrutura de hábitat é o fator mais importante para determinar a comunidade de pequenos mamíferos no Cerrado. Essas diferenças parecem ser função das características locais dos mosaicos, como também diferenças entre bacias hidrográficas, ou ainda, diferenças entre hábitats florestados localizados nos platôs altos comparados com matas de vales em depressão, ou diferenças detectadas em porções de solos úmidos de Cerrado com abundância de gramíneas, comparados com microhábitats de solos secos e pedregosos.

Palavras-chave: Cerrado, conservação, hábitats, marsupiais, pequenos mamíferos, roedores.

INTRODUCTION

The Cerrado biome of central Brazil comprises savanna-like vegetation, ranging from open grassland to closed-canopy forested savanna and even true forest along rivers. It originally covered nearly two million km², and is the second largest Brazilian biome after Amazonia (EITEN, 1972; 1993; RIBEIRO & WALTER, 1998, 2001).

The region is not homogeneous in geology, soils, and vegetation cover, which varies from site to site (FELFILI *et al.*, 1994; FURLEY, 1996). It is very easy to cross markedly different kinds of habitats within a distance of only 100-200 meters, from dense gallery forest, through open wet bog and

mesic grassland, to arboreal savanna. The patterns of habitat intergradation are even more complex in ecotone zones of broad contact between biomes (Cerrado-Amazonia to the north; Cerrado-Caatinga to the northeast; Cerrado-Atlantic Forest to the east, and Cerrado-Pantanal to the west). These contact zones vary from moist to semi-arid regions. The intensive human occupation of the Cerrado biome started in 1960, after the inauguration of Brasília, the Nation's new capital. Cattle ranching and, more recently, soybean plantations are the major land use activities (ALHO & MARTINS, 1995; ALHO, *in press*).

This highly mosaic biome is home to endemic plant species and patchily distributed animals. For

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example, it is common to find small mammal species with a preference for forest habitats or for open habitats within the same study area. In the gallery forest, surrounded by open savanna habitats, forest-dwelling arboreal genera such as *Oecomys, Oryzomys, Oligoryzomys*, and *Rhipidomys* occur within a few meters of open-habitat dwellers such as *Bolomys* and *Oxymycterus*. The genus *Oligoryzomys* also occur in both open and forested habitats. Despite many significant contributions to our knowledge of Cerrado ecology, small mammal distribution and habitat use over the last two decades, the community dynamics and use of space by species within this mosaic landscape are still incompletely understood.

The objective of this review is to document the distribution of small mammals in different kinds of habitats within the Cerrado landscape, to evaluate the relative contribution of the biome to faunal knowledge, to relate the distribution of these species to the mosaic of habitats, and to highlight conservation challenges.

MATERIAL AND METHODS

The savanna vegetation known as Cerrado sensu lato (spelled herein with upper-case initial) comprises a variety of different habitats (EITEN, 1972, 1993; RIBEIRO & WALTER, 1998, 2001). Open savannas are termed "campo", ranging from campo limpo (literally "clean field": grassland without shrubs or trees), through campo sujo ("dirty field", with scattered small shrubs), to campo cerrado (savanna with a scattered cover of gnarled trees); wet campo occurs on permanently moist soils. Open-canopy wooded savanna with a grassy understory is known as cerrado sensu stricto (lower-case initial), whereas tall, dense, forested savanna with a closed or semiclosed canopy is cerradão. True forest penetrates deep into the Cerrado landscape in narrow bands along rivers and creeks (gallery forests, riverine forests); semi-deciduous mesophytic forest may also be found on well-drained upland slopes. The floristic composition of cerrado, cerradão, mesophytic forest, and gallery forest differs from that of the wet forests with palm trees, locally known as veredas, that are located in waterlogged valley bottoms within the Cerrado (RATTER, 1986; EITEN, 1972, 1993).

This review of small mammal ecology in the Cerrado is based on information presented in published works and graduate dissertations, most of which have been produced during the last twenty years.

RESULTS AND DISCUSSION

Small mammal species show a high degree of habitat fidelity in their distribution within the Cerrado landscape (ALHO, 1981, 1993; ALHO et al., 1986; OLIVEIRA, 1993; REIS, 1993; TALAMONI, 1996; GASTAL, 1997; LACHER & ALHO, 2001; PALMA, 2002). Habitat is an important factor in community structure: species occurring in forested habitats (gallery forests, riverine forests, mesophytic forests, and cerradão) show considerable habitat differences, as do those occupying open savanna habitats (cerrado, campo, wet campo, campo sujo, campo cerrado). The same pattern is also observed when taxonomic groups such as marsupials, murids or echimyids are analyzed (LACHER & ALHO, 2001; PALMA, 2002). Most field work carried out by researchers in the Cerrado is based on trapping along transects through sampling habitats or in grids of capture stations for capture-mark-release-recapture programs. Generally there are substantial differences in the success rates of trap lines along transects or in grids, depending on the kind of habitats (forested habitats have lower rates) and the season (the dry season peak of seeding grasses results in more individual recruitment of open habitat dwellers). Thus, capture success is not homogeneous within the habitats, ranging from 2% to 8% of total trap-nights, 5% being a good success rate. Additionally, different methods may suggest different population sizes: for instance, pit fall traps differ from Sherman traps, and some species, such as Cavia aperea, tend to avoid traps altogether. Intensive capture-recapture routines indicated that small mammals were caught in close proportion to their occurrence in a given sample habitat (ALHO, 1981, 1993; ALHO et al., 1986; OLIVEIRA, 1993; REIS, 1993; TALAMONI, 1996; GASTAL, 1997; LACHER & ALHO, 2001; PALMA. 2002).

The distribution of small mammal species among available habitats, based on transitions of vegetation types, reveals that there are habitat generalists and habitat specialists (Tab.1). Three marsupials (Monodelphis domestica, Monodelphis americana, and Didelphis albiventris) are categorized as habitat generalists since they are usually captured in more than three types of habitats. The common opossum Didelphis albiventris is caught in gallery forest, cerrado, campo cerrado, and cerradão, and also is commonly seen alive or killed by cars in Brasília and other cities.

 $Table \ 1. \ Species \ list of small \ mammals \ by \ habitat \ according \ to \ intensive \ capture-mark-recapture \ field \ work \ surveying \ the \ Cerrado \ landscape.$

Species	Habitats	Sources
RODENTS - HABITAT GENERALIST	S	
Bolomys lasiurus	Cerrado (s.s.); campo; wet campo; campo-cerrado	Alho <i>et al.</i> , 1986; Lacher & Alho, 2001; Palma, 2002
Oryzomys subflavus	Ecotones of Cerrado and Atlantic Forest and of Cerrado and Caatinga - cerrado (s.s.); wet campo; campo-cerrado; gallery forest	Langguth & Bonvicino, 2002; Bonvicino, 2003; Alho <i>et al.</i> , 1986 Lacher & Alho, 2001; Palma, 2002
Oryzomys scotti	Cerrado (s.s.); campo; wet campo; campo-cerrado.	Langguth & Bonvicino, 2002; Bonvicino, 2003.
Oryzomys maracąjuensis	Cerrado (s.s.); campo; wet campo; campo-cerrado.	Langguth & Bonvicino, 2002; Bonvicino, 2003.
Oryzomys marinhus	Cerrado (s.s.); campo; wet campo; campo-cerrado.	Langguth & Bonvicino, 2002; Bonvicino, 2003.
MARSUPIALS – HABITAT GENERALIS	STS	
Monodelphis domestica	Cerrado (s.s.); campo; campo cerrado; wet campo; gallery forest	Alho <i>et al.</i> , 1986; Lacher & Alho, 2001; Palma, 2002
Didelphis albiventris	Cerrado (s.s.); campo; campo- cerrado; gallery forest; mesophytic forest	Alho <i>et al.</i> , 1986; Lacher & Alho, 2001; Palma, 2002
Monodelphis americana	Cerrado (s.s.); campo; campo- cerrado; gallery forest	Alho <i>et al.</i> , 1986; Lacher & Alho, 2001; Palma, 2002
RODENTS - HABITAT SPECIALISTS		
Akodon lindberghi (listed as Plectomys paludicola)	Gallery forest	Alho et al., 1986
Akodon cursor	Gallery forest; mesophytic forest; cerradão	Alho <i>et al.</i> , 1986; Mares & Ernest, 1995; Gastal, 1997; Palma, 2002
Akodon montensis	Campo; cerradão; gallery forest.	Oliveira, 1993; Talamoni, 1996
Calomys expulsus	Campo; cerrado (s.s.).	Bonvicino & Almeida, 2000; Bonvicino <i>et al.</i> , 2003; Oliveira, 1993; Palma, 2002.
Calomys tener	Campo; cerrado (s.s.).	Bonvicino & Almeida, 2000; Bonvicino <i>et al.</i> , 2003; Oliveira, 1993; Palma, 2002.
Calomys tocantinsi	Cerrado (s.s.); campo.	Bonvicino & Almeida, 2000; Bonvicino <i>et al.</i> , 2003.
Nectomys squamipes	Gallery forest	Gastal, 1997; Palma, 2002
Oecomys bicolor	Gallery forest; cerradão	Gastal, 1997; Palma, 2002
Oecomys cleberi	Gallery forest	Locks, 1981
Oecomys concolor	Gallery forest	Gastal, 1997; Palma, 2002
Oligoryzomys microtis	Gallery forest with influence of Amazonia (= vereda); wet campo	Lacher & Alho, 2001.
Oligoryzomys stramineus	Gallery forest	Talamoni, 1996; Gastal, 1997; Palma, 2002

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SPECIES	Habitats	Sources
RODENTS - HABITAT SPECIALISTS		
Oligoryzomys fornesi	Gallery forest; cerrado (s.s.) and cerradão.	Myers <i>et al.</i> , 1995.
Oligoryzomys nigripes (= O. eliurus)	Gallery forest; cerrado (s.s.) and cerradão.	Myers & Carleton, 1981; Talamoni, 1996; Gastal, 1997; Lacher & Alho 2001; Palma, 2002
Oryzomys megacephalus (= O. capito)	Gallery forest	Talamoni, 1996; Gastal, 1997; Palma, 2002
Oxymycterus delator	Gallery forest	Palma 2002
Oxymycterus roberti	Wet campo	Gastal, 1997; Lacher & Alho, 2001
Pseudoryzomys simplex	Campo-cerrado	Talamoni, 1996
Proechimys longicaudatus	Gallery forest (valley forest)	Gastal, 1997; Lacher & Alho, 2001 Palma, 2002
Clyomys laticeps	Cerrado (s.s.)	Palma, 2002
Trichomys apereoides	Cerrado (s.s. – rocks)	Lacher & Alho, 2001; Palma, 2002
Cavia aperea	Campo-cerrado; wet campo	Alho et al., 1986; Talamoni, 1996; Gastal, 1997
Rhipidomys mastacalis	Gallery forest (valley forest); cerradão.	Tribe, 1996; Gastal, 1997; Lacher & Alho, 2001; Palma, 2002
Rhipidomys macrurus	Gallery forest (valley forest); cerradão.	Tribe, 1996.
Euryzygomatomys spinosus (= E. guiara)	Cerrado (s.s.); campo-cerrado	Woods, 1993; Lacher & Alho, 2001
Thalpomys lasiotis	Cerrado (s.s.)	Alho <i>et al.</i> , 1986
Thalpomys cerradensis	Cerrado (s.s.)	Palma, 2002
Neacomys spinosus	Gallery forest	Lacher & Alho, 2001
Wiedomys pyrrhorhinos	Cerrado (s.s.)	Reis, 1993
MARSUPIALS – HABITAT SPECIALISTS		
Caluromys lanatus	Mesophytic forest	Talamoni, 1996
Caluromys philander	Gallery forest	Lacher & Alho, 2001; Palma, 2002
Gracilinanus agilis	Cerradão; gallery forest (valley forest)	Gastal, 1997; Lacher & Alho, 2001 Palma, 2002
Micoureus demerarae	Gallery forest (valley forest)	Lacher & Alho, 2001; Palma, 2002
Philander opossum	Gallery forest	Alho et al., 1986; Palma, 2002
Marmosops noctivagus	Gallery forest (valley forest)	Lacher & Alho, 2001
Marmosa murina	Gallery forest (wet forest)	Lacher & Alho, 2001
Chironectes minimus	Gallery forest	Alho <i>et al.</i> , 1986; Mares & Ernest, 1995
Thylamys velutinus	Cerrado (s.s.)	Vieira & Palma, 1996
Thylamys karimii	Cerrado (s.s.)	Reis, 1993

Generalist rodents (Bolomys lasiurus and Oryzomys subflavus), are caught in more than three different open habitats. Taxonomic studies have shown that this so-called *Oryzomys subflavus* is in reality a group of species: while *O. subflavus* is found in the ecotones of the Cerrado with the Atlantic Forest and the Caatinga, O. scotti is found in the Cerrado of central Brazil, where O. maracajuensis and O. marinhus also occur (LANGGUTH & BONVICINO 2002; BONVICINO, 2003). Bolomys lasiurus is one of the most common terrestrial small mammal species of the cerrado s.s. Its species density is around 11 individuals per hectare and home range sizes vary from 200 to 2,500m², most of the adult animals occupying an area of around 800m²; the areas occupied by adult males overlap with those of adult females more than with other groups of the same species, such as juveniles (ALHO & SOUZA, 1982). The average greatest displacement recorded for species, considering four or more recaptures, varies from 9m for Akodon cursor to 54m for Gracilinanus agilis, but the greatest movements of most species are between 20 and 40 m within their home range areas (GASTAL, 1997). Some recently described rodent species such as Akodon lindberghi, Thalpomys cerradensis, and Microakodontomys transitorius appear to be very restricted to their habitats and are rarely listed in field works. This may be due to the patchy nature of the Cerrado landscape, which probably led to the loss of the habitat of Juscelinomys candango, described by Moojen in 1965.

Among the species that occur in all forested habitats (Tab.1), habitat preference varies among different types of gallery forests, riverine forests (mata ciliar), mesophytic forest, and forested savanna (cerradão). Surveys in cerradão are scarce, and data on community composition for this habitat is, therefore, still incomplete. Small mammals occurring in open habitats, including arboreal savanna (cerrado) and all kinds of grasslands (campos) are either generalists (with a wide range of habitat use) or specialists (with habitat specificity).

Sex ratios of small mammals do not differ significantly from 1:1. Species show a rapid turnover in the study areas, with few animals persisting for one year (ALHO & SOUZA, 1982; MARES & ERNEST, 1995; GASTAL, 1997). Persistence of marked individuals in different study areas varies from 2 to 12 months from the first to the last capture. Mean persistence varies from 2 to 4 months. GASTAL (1997) reports a *Cavia aperea* recorded for 14 months in Brasília.

Reproductive activities and young individuals recorded in the surveys indicate, in general, reproduction throughout the year, but with peaks during the dry and/or wet seasons, depending on the species. Bolomys lasiurus has a peak in May-June. Rhipidomys displays three peaks: June-July (dry period), November-December (wet period), and August-September (dry period), whereas females of Proechimys are more sexually active in September-October (end of the dry season), according to GASTAL (1997). Small mammal biomass is greatest during the dry season (peaking in October, the end of dry period) both for forest dwellers and open habitat dwellers (GASTAL, 1997). Detailed analysis using different methods has shown a high degree of habitat specificity for small mammals in open and forested habitats of the Cerrado landscape (NITIKMAN & MARES, 1987; LACHER & ALHO, 1989; LACHER et al., 1989; HENRIQUES & ALHO, 1991; ALHO, 1993; MARES & ERNEST, 1995; TALAMONI, 1996; GASTAL, 1997; LACHER & ALHO, 2001; PALMA, 2002). Some studies have shown quantitative habitat variables which correlate with species richness and abundance of Cerrado small mammal species, including microhabitat components (ALHO, 1981; ALHO et al. 1986; LACHER et al. 1989; HENRIQUES & ALHO, 1991; LACHER & ALHO, 2001). A clear association between small mammal density and kind of habitats has been shown (GASTAL, 1997; TALAMONI, 1996; LACHER & ALHO, 2001; PALMA, 2002). Community compositions differ between two grassland habitats: drier habitat has fewer species, with 38% of the overall population density of the more mesic formation. Oxymycterus roberti, for example, prefers a narrow range of habitat within the Cerrado, being restricted to the moister portion of the grassland that has soft soil and abundant grass Tristachia leostachya (LACHER et al., 1989).

Population parameters of gallery forest dwellers (Didelphis albiventris, Gracilinanus agilis, Philander opossum, Akodon cursor, Nectomys squamipes, Oligoryzomys nigripes, Oecomys bicolor, Oryzomys capito, Rhipidomys mastacalis, and Proechimys roberti), such as species richness, diversity, and biomass, are correlated with forest basal area, whereas the evenness of the total small mammal fauna is correlated with vegetation cover (GASTAL, 1997). In addition, species richness and diversity are correlated to gallery forest complexity, expressed by vertical habitat diversity.

When two sympatric rodent species are examined (Bolomys lasiurus and Oxymycterus roberti) for eight simultaneous microhabitat variables, patterns of habitat utilization and species relationships are distinct. The two species differ markedly in three microhabitat variables: plant species richness, forb ground cover, and distance to the nearest tree or shrub. While Bolomys is more a generalist, Oxymycterus is more a specialist associated with less diverse lower forbs, shrub, tree cover and higher ground cover (HENRIQUES & ALHO, 1991). Small mammals have the ability to explore the vertical strata of the habitat. Some genera are essentially arboreal, such as Oecomys and Rhipidomys. Experimental work carried out in a laboratory setting to test the scansorial and particularly the climbing ability of Oligoryzomys nigripes (formerly O. eliurus) and Oryzomys subflavus (Oryzomys subflavus species group) has demonstrated these species' ability to explore the arboreal stratum. They ascend trees using their tails as balancing aids: the animal keeps its tail stretched parallel to the branch when climbing. Oligoryzomys nigripes exhibits better arboreal performance than Oryzomys subflavus (ALHO & VILLELA, 1984).

The combination of vegetation type and substrate structured the community of 19 terrestrial species studied in the Cerrado of Mato Grosso into several smaller communities with little faunal overlap (LACHER & ALHO, 2001). This study showed that most species were captured in only one or two of the qualitative habitat types. There were openhabitat species that were completely absent from forest, and forest species that were captured only in forest habitats. Additional cluster analysis of those 19 species confirmed the separation made by qualitative classification of habitats based on plant species composition and other habitat characteristics. The results for habitat associations of small mammal species determined by cluster analysis of soil and vegetation structural characteristics (independently of plant species composition) generated five fairly distinct clusters. The gallery forest cluster grouped the same set of species that had previously been assigned to gallery spinosus, forest (Neacomys Oruzomus megacephalus, Nectomys squamipes, Oecomys bicolor, Proechimys longicaudatus, and Caluromys philander), confirming the earlier analysis. The cluster analysis also grouped the six species that had previously been associated with wet campo (Oligoryzomys microtis — occurring at the Cerrado-

Amazonia contact zone, Oligoryzomys nigripes (= eliurus), Oryzomys subflavus species group, Bolomys lasiurus, Monodelphis domestica, and Marmosa murina). The grouping of species was essentially the same whether it was done qualitatively by habitat type or by a quantitative analysis of structural aspects of the vegetation and substrate of the habitat (LACHER & ALHO, 2001). Small mammals of the Cerrado show a distinct population fluctuation as a function of marked seasonality (dry and wet seasons). Bolomys lasiurus, for example, shows a recruitment of young into populations when there is abundance of Cerrado grass seeds (at the end of the wet season and beginning of the dry season), and five species of gallery forest dwellers (Oecomus bicolor, Oecomus concolor, Oligoryzomys nigripes, Rhipidomys mastacalis, and Gracilinanus agilis) display peaks during the wet season and population decline during the dry season, although this pattern is not clear for all species (ALHO et al., 1986; MARES & ERNEST, 1995). While Oecomys bicolor densities peak at the end of the dry season, Oecomys concolor presents greater density in the middle of the dry season (GASTAL, 1997). Both species are arboreal but O. bicolor uses the upper stratum (more than 80% of captures occur in trees) while O. concolor uses the stratum closer to the ground. In surveys comparing disturbed and undisturbed canopies in gallery forests, Oecomys bicolor proves to be sensitive to habitat modification by occurring at lower densities (PALMA, 2002). When the same analysis is carried out for disturbance of the forest understory, all species are affected.

Nectomys squamipes is only captured in the interior of the gallery forest, in habitat associated with water. Peaks of species abundance, biomass and richness occur at the beginning of the dry season, when Bolomys lasiurus in the open habitats and Proechimys roberti in the gallery forest are the dominant species (GASTAL, 1997). The species of Oligoryzomys are associated with the gallery forest but O. microtis is found at the forest edge in the Cerrado-Amazonia contact zone (LACHER & ALHO, 2001).

In large-scale analyses, such as comparisons among different river basins, small mammal communities differ in composition and abundance (LACHER & ALHO, 2001; PALMA, 2002). The latter author concluded that the small mammal communities of the Tocantins river basin are different from those of the Paraná/São Francisco river basins; the differences are more notable between basins rather than within basins. While the Paraná/São Francisco

communities are composed of essentially the same species, the Tocantins community has a greater number of species, particularly marsupials. Differences were also detected between small mammal communities of plateaus (above 900m) and lowland depressions (PALMA, 2002). In addition, the larger and the more pristine the forested habitats, the greater is the number of small mammal species in the community.

The small mammal community stays intact until a drastic habitat disturbance affects habitat integrity, for example inundation due to the formation of a reservoir for a hydroelectric plant (ALHO et al., 2003). All these findings appear to be consistent with the mosaic aspect of different niches present within the Cerrado biome. It is still too early to pursue a unifying conclusion on the Cerrado small mammal community assemblage, although current knowledge has opened the door to discussions of community organization. Large-scale habitat disturbances, such as the use of fire and the conversion of natural vegetation into pasture or sovbean plantations, have the potential to alter population parameters, community structure, use of space and other ecological requirements of the Cerrado small mammal assemblages. Patches of cerradão, for example, are rapidly disappearing as natural vegetation is converted into agricultural land or pastures for cattle ranching, since the soils in these areas are generally richer in nutrients. Such environmental alterations can damage habitat specialists and benefit pan-habitat species, changing community composition associated with pristine habitat gradients in the Cerrado landscape. Bolomys lasiurus, for example, has adopted peri-urban habits and is found in areas of human occupation inhabiting natural habitats recently converted into crop fields, and recently it has been incriminated in the spread of hantavirus. In the outskirts of Brasília in 2004, the Health Service of the Federal District confirmed 37 cases of the disease in humans with 16 deaths.

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